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# The Role of Nutrient Efficient Plants in Improving Crop Yields in the Twenty First Century

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## ABSTRACT

In the 21st century, nutrient efficient plants will play a major role in increasing crop yields compared to the 20th century, mainly due to limited land and water resources available for crop production, higher cost of inorganic fertilizer inputs, declining trends in crop yields globally, and increasing environmental concerns. Furthermore, at least 60% of the world's arable lands have mineral deficiencies or elemental toxicity problems, and on such soils fertilizers and lime amendments are essential for achieving improved crop yields. Fertilizer inputs are increasing cost of production of farmers, and there is a major concern for environmental pollution due to excess fertilizer inputs. Higher demands for food and fiber by increasing world populations further enhance the importance of nutrient efficient cultivars that are also higher producers. Nutrient efficient plants are defined as those plants, which produce higher yields per unit of nutrient, applied or absorbed than other plants (standards) under similar agroecological conditions. During the last three decades, much research has been conducted to identify and/or breed nutrient efficient plant species or genotypes/cultivars within species and to further understand the mechanisms of nutrient efficiency in crop plants. However, success in releasing nutrient efficient cultivars has been limited. The main reasons for limited success are that the genetics of plant responses to nutrients and plant interactions with environmental variables are not well understood. Complexity of genes involved in nutrient use efficiency for macro and micronutrients and limited collaborative efforts between breeders, soil scientists, physiologists, and agronomists to evaluate nutrient efficiency issues on a holistic basis have hampered progress in this area. Hence, during the 21st century

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agricultural scientists have tremendous challenges, as well as opportunities, to develop nutrient efficient crop plants and to develop best management practices that increase the plant efficiency for utilization of applied fertilizers. During the 20th century, breeding for nutritional traits has been proposed as a strategy to improve the efficiency of fertilizer use or to obtain higher yields in low input agricultural systems. This strategy should continue to receive top priority during the 21st century for developing nutrient efficient crop genotypes. This paper over views the importance of nutrient efficient plants in increasing crop yields in modern agriculture. Further, definitions and available methods of calculating nutrient use efficiency, mechanisms for nutrient uptake and use efficiency, role of crops in nutrient use efficiency under biotic and abiotic stresses and breeding strategies to improve nutrient use efficiency in crop plants have been discussed.

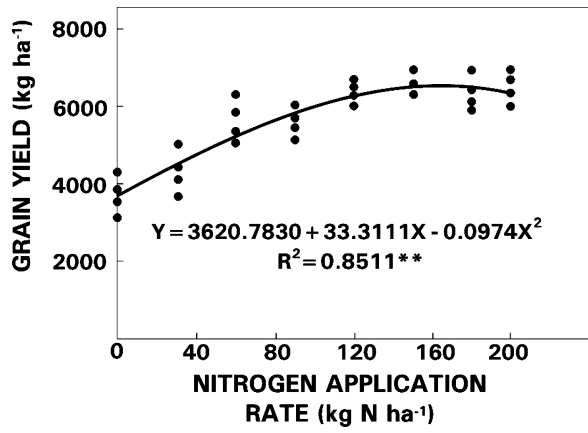
**Keywords:** abiotic and biotic stress, crop species, grain yield, nutrient use efficiency, root geometry

## INTRODUCTION

Mineral nutrition alone has contributed significantly to increased crop yields during the 20th century. Borlaug and Dowsell (1994) reported that 50% of the increase in crop yields worldwide during the 20th century was due to application of chemical fertilizers. These authors also reported that during the 21st century, the essential plant nutrients would be the single most important factor limiting crop yields, especially in developing countries. Borlaug and Dowsell (1997) state that science based commercial agriculture is a 20th century invention. Loneragan (1997) states that knowledge generated during the 20th century in the field of mineral nutrition has impacted on current food production and provided information needed for further advances for the 21st century.

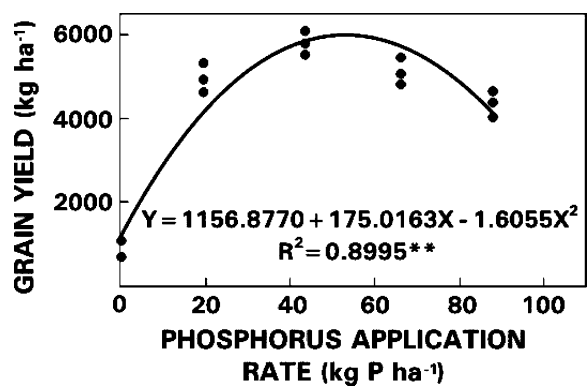
During (1950 to 1990), grain yields of cereals such as wheat (*Triticum aestivum* L.), maize (*Zea mays* L), and rice (*Oryza sativa* L) tripled worldwide. Wheat yields in India, for example, increased by nearly 400% from 1960 to 1985, and yields of rice in Indonesia and China more than doubled. This vastly increased production resulted from high yielding varieties, improved irrigation facilities and use of chemical fertilizers. The results were very significant in Asia and Latin America, where the term “green revolution” was used to describe the process (Brady and Weil, 2002). The increase in productivity of annual crops with the application of fertilizers and lime in the Brazilian Cerrado or savanna region during the 1970s and 1980s is another example of 20th century expansion of the agricultural frontier in acid soils (Borlaug and Dowsell, 1997).

Stewart et al. (2005) reported that in the 20th century the average percentage of yield attributable to fertilizer generally ranged from about 40 to 60% in the USA and England and tended to be much higher in the tropics. Further, they concluded that in the USA omission of nitrogen (N) decreased corn yield by 41% and elimination of N in cotton production resulted in an estimated yield reduction of 37%. These authors also reported that if effect of other nutrient



**Figure 1.** Relationship between nitrogen rate and grain yield of lowland rice grown on Brazilian Inceptisol. *Source:* Fageria, unpublished data.

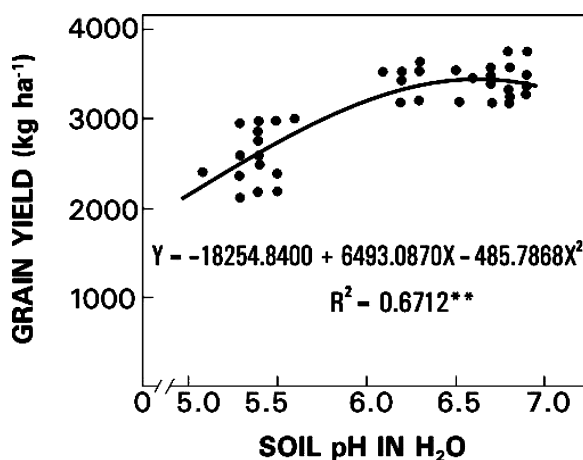
inputs such as phosphorus (P) and potassium (K) been measured, the estimated yield reductions would have probably been greater. Baligar et al. (2001) reported that as much as half of the rise in crop yields during the 20th century resulted largely from increased use of fertilizers. Fageria and Baligar (2001) and Fageria et al. (1997) reported significant increase in grain yields of lowland rice in Brazilian Inceptisols with the application of N and P. Figures 1 and 2 show significant increases in grain yields of lowland rice with the application of N and P fertilizers in a Brazilian Inceptisol. Nitrogen was responsible for 85% of the variation in grain yield and phosphorus was responsible for 90% variation in grain yield. Such findings highlight the importance of nitrogen and phosphorus



**Figure 2.** Relationship between phosphorus application rate and grain yield of lowland rice grown on Brazilian Inceptisol. *Source:* Fageria, unpublished data.

inputs in enhancing lowland rice production in Brazilian Inceptisols. Further, Fageria and Baligar (1997a) reported that in Brazilian Oxisols N, P, and zinc (Zn) were the most limiting nutrients for annual crops.

Soil acidity, alkalinity and salinity, anthropogenic activities, monoculture farming and wind and water erosion processes are the major degradation factors for cultivated soils (Dudal, 1982; Gupta and Abrol, 1990; Lal, 1990; Clark and Baligar, 2000). These processes have lowered the fertility and productivity of many cultivated soils of the world. Close to 4 billion ha of the world's soils are classed as acidic. The total area of salt affected soils in the world is about 950 million ha. A majority of the world population makes a living on areas covered by acidic and salt affected soils, and therefore, increases in crop productivity of these soils is of a paramount concern. The poor productivity of crops grown in acid and salt affected soils is mainly due to combinations of elemental toxicities and deficiencies or unavailability of essential nutrients (Gupta and Abrol, 1990; Baligar and Fageria, 1997; Grattan and Grieve, 1999ab). Addition of fertilizers and amendments (particularly lime) are essential in achieving proper nutrient supply and maximizing yields in these soils (Figure 3). However, efficiency of applied fertilizers is very low. The efficiency of acquisition, transport and utilization of nutrients varies with crop species and genotype/cultivar within species, and their interactions with the environment (Baligar and Fageria, 1999; Baligar et al. 2001). Acid and alkaline soil constraints on plant mineral nutrition have been covered extensively by Clark and Baligar (2000). Further, they also states the existence and development of considerable germplasm with improved ability to grow and produce under mineral stress In acid and salt affected soils, improving efficiency in recovery of applied nutrients is becoming a prerequisite



**Figure 3.** Relationship between soil pH and grain yield of common bean grown on Brazilian Oxisol. *Source:* Fageria et al. (2004a).

to lower production costs, improvement crop yields, and reduction in degradation of the environment.

Increasing world population and projection of better income of the majority of world populations, especially in Asia, are putting heavy pressure on the available arable land (Brown, 1997). The world's total demand for food is likely to nearly double its present level by 2030, and there is limited new land available for expansion of cultivation to achieve this production level (Brown, 1997). Therefore, more food has to be produced from the presently available arable land rather than incorporating new land for cultivation. Increasing crop yield potentials per unit of land is an urgent concern. The higher nutrient use efficiency in plants must be fully explored to increase food production to feed the growing human population, and this has to be achieved without accelerating environmental degradation from excessive fertilizer use (Evans, 1998; Epstein and Bloom, 2005). The objective of this article is to discuss the importance of nutrient efficient plants in improving crop yields during the 21st century.

### **DEFINITIONS FOR NUTRIENT EFFICIENT PLANTS AND NUTRIENT USE EFFICIENCY**

Nutrient efficient plants as well as nutrient use efficiency in plants have been defined in several ways. Large variations in defining nutrient efficient plants and methods used in calculating nutrient use efficiency, makes it difficult to compare results of different studies. The effort to measure yield response to an applied nutrient is further confounded by other factors, such as variable soil fertility levels, climatic conditions, crop rotations, and changes in production practices that affect nutrient use efficiency (Stewart et al., 2005). In simple terms, efficiency is the ratio of output (economic yield) to input (fertilizers) for a process or complex system (Crop Science Society of America, 1992). Some of these definitions pertaining to two subjects (nutrient efficient plants and nutrient use efficiency), reported in the literature, are presented and discussed in Tables 1 and 2. Various nutrient use efficiency expressions for lowland rice genotypes under Brazilian conditions are given in Table 3. Figures 4 and 5 show responses of lowland rice genotypes to N and P fertilization. Three genotypes showed linear responses and two genotypes showed quadratic response to increasing levels of applied N (Figure 4). All three genotypes showed quadratic response to increasing levels of applied P (Figure 5). Yields of these genotypes varied under low as well as under higher N and P rates, indicating different use efficiency of applied N and P.

Nitrogen recovery efficiency in annual crops averages only about 42% and 29% in developed and developing countries, respectively (Raun and Johnson, 1999). Similarly, Fageria and Baligar (2005) reported that N recovery efficiency in crop plants is usually less than 50% worldwide. This low nutrient recovery efficiency is associated with loss of applied nutrients by leaching, volatilization,

Table 1  
Definitions of nutrient efficient plants

Definition	Reference
Nutrient efficient plant is defined; a plant that absorbs, translocates, or utilizes more of a specific nutrient than another plant under conditions of relatively low nutrient availability in the soil or growth media.	Soil Science Society of America (1997)
The nutrient efficiency of a genotypes (for each element separately) is defined as the ability to produce a high yield in a soil that is limiting in that element for a standard genotype.	Graham (1984)
Nutrient efficiency of a genotype/cultivar is defined as the ability to acquire nutrients from a growth medium and/or to incorporate or utilize them in the production of shoot and root biomass or utilizable plant material (grain).	Blair (1993)
An efficient genotype is one which absorbs relatively high amounts of nutrients from soil and fertilizer, produces a high grain yield per unit of absorbed nutrient and stores relatively little nutrients in the straw.	Isfan (1993)
Efficient plants are defined as those that produce more dry matter or have a greater increase in harvested portion per unit time, area, or applied nutrient, have fewer deficiency symptoms, or have greater incremental increases and higher concentrations of mineral nutrients than other plants grown under similar conditions or compared to a standard genotype.	Clark (1990)
Efficient germplasm requires less nutrients than an inefficient one for normal metabolic processes	Gourley et al. (1994)
Efficient plant is defined as one that produces higher economic yield with a determined quantity of applied or absorbed nutrient compared to other or a standard plant under similar growing conditions	Proposed in this paper

denitrification, and soil erosion (Fageria and Baligar, 2005). In addition, use of inadequate crop management practices, biotic and abiotic stresses are also responsible for low nutrient use efficiency.

**MECHANISMS INVOLVED IN NUTRIENT UPTAKE  
AND USE EFFICIENCY**

Significant variation exists among crop species and genotypes of the same species in nutrient uptake and utilization (Gerloff and Gabelman1983; Baligar et al., 1990; Baligar et al., 2001; Epstein and Bloom, 2005; Fageria and Baligar,

Table 2  
Definitions and methods of calculating nutrient use efficiency.

Designation of efficiency	Definitions and formulas for calculation
Agronomic efficiency (AE)	The agronomic efficiency is defined as the economic production obtained per unit of nutrient applied. It can be calculated by. $AE (kg\ kg^{-1}) = (G_f - G_u/N_a)$ , where $G_f$ is the grain yield of the fertilized plot (kg), $G_u$ is the grain yield of the unfertilized plot (kg), and $N_a$ is the quantity of nutrient applied (kg).
Physiological efficiency (PE)	Physiological efficiency is defined as the biological yield obtained per unit of nutrient uptake. It can be calculated by. $PE (kg\ kg^{-1}) = (BY_f - BY_u/N_f - N_u)$ , where, $BY_f$ is the biological yield (grain plus straw) of the fertilized pot (kg), $BY_u$ is the biological yield of the unfertilized plot (kg), $N_f$ is the nutrient uptake (grain plus straw) of the fertilized plot, and $N_u$ is the nutrient uptake (grain plus straw) of the unfertilized plot (kg).
Agrophysiological efficiency (APE)	Agrophysiological efficiency is defined as the economic production (grain yield in case of annual crops) obtained per unit of nutrient uptake. It can be calculated by. $APE (kg\ kg^{-1}) = (G_f - G_u/N_f - N_u)$ , where, $G_f$ is the grain yield of fertilized plot (kg), $G_u$ is the grain yield of the unfertilized plot (kg), $N_f$ is the nutrient uptake (grain plus straw) of the fertilized plot (kg), $N_u$ is the nutrient uptake (grain plus straw) of unfertilized plot (kg).
Apparent recovery efficiency (ARE)	Apparent recovery efficiency is defined as the quantity of nutrient uptake per unit of nutrient applied. It can be calculated by. $ARE (\%) = (N_f - N_u/N_a) \times 100$ , where, $N_f$ is the nutrient uptake (grain plus straw) of the fertilized plot (kg), $N_u$ is the nutrient uptake (grain plus straw) of the unfertilized plot (kg), and $N_a$ is the quantity of nutrient applied (kg).
Utilization efficiency (EU)	Nutrient utilization efficiency is the product of physiological and apparent recovery efficiency. It can be calculated by; $EU (kg\ kg^{-1}) = PE \times ARE$
Nutrient efficiency ratio (NER)	Gerloff and Gabelman (1983) to differentiate genotypes suggested nutrient efficiency ratio into efficient and inefficient nutrient utilizers. It can be calculated by using the formula. $NER (kg\ kg^{-1}) = (\text{Yield in kg/amount of nutrient in plant tissue in kg})$ .



Table 3  
Nitrogen use efficiency in lowland rice genotypes

Genotype	AE (kg kg <sup>-1</sup> )	PE (kg kg <sup>-1</sup> )	APE (kg kg <sup>-1</sup> )	ARE (%)
CNAi 8886	23	105	56	37
CNAi 8569	17	188	69	29
BRS GO Guará	21	222	123	29
BRS Jaburu	16	114	64	26
BRS Biguá	19	145	74	23
Average	19	155	77	29

AE = Agronomic efficiency, PE = Physiological efficiency, APE = Agrophysiological efficiency, and ARE = Apparent recovery efficiency.

Source: Fageria et al. (2006b).

2005). For example, the siliceous and calcareous sandy soils of South Australia, are considered severely deficient in micronutrients for growth of wheat, oats (*Avena sativa* L.), or barley (*Hordeum vulgare* L), but, growth and yield of rye (*Secale cereale* L.) was optimal on these soils (Graham, 1984). The native vegetation in this area is fully adapted to these soils mainly due to their slow growth rate (Loneragan, 1978). The difference in nutrient uptake and utilization

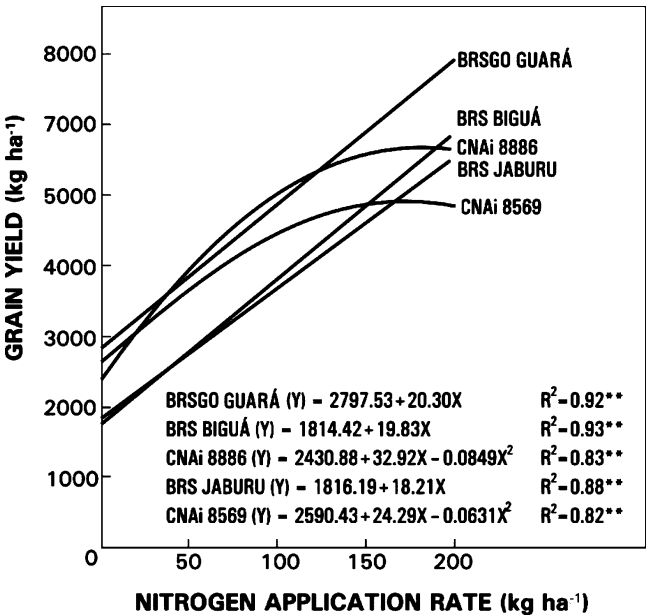
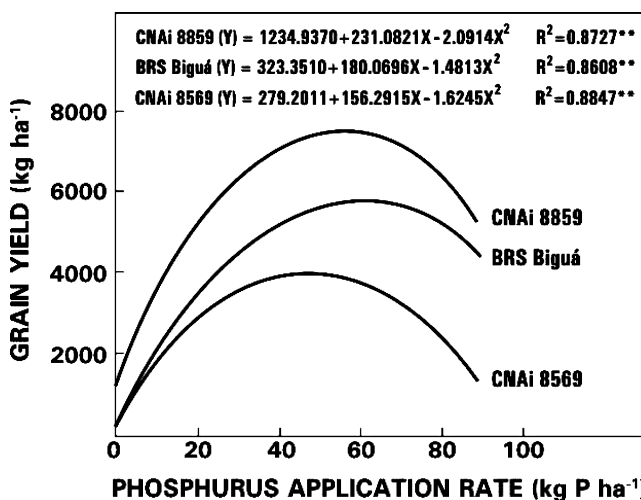


Figure 4. Response of five lowland rice genotypes to nitrogen fertilization applied to Inceptisol. Source: Fageria and Baligar (2006).



**Figure 5.** Response of lowland rice genotypes to phosphorus fertilization. *Source:* Fageria, unpublished data.

may be associated with better root geometry, ability of plants to take up sufficient nutrients from lower or subsoil concentrations, plants ability to solubilize nutrients in the rhizosphere, better transport, distribution and utilization within plants and balanced source-sink relationships (Graham, 1984; Baligar et al., 2001; Fageria and Barbosa Filho, 2001; Fageria and Baligar, 2003). The antagonistic (uptake of one nutrient is restricted by another nutrient) and synergistic (uptake of one nutrient is enhanced by other nutrient) effects of nutrients on nutrient use efficiency among various plant species and cultivars within species have not been well explored.

### Better Root Geometry

Plants, having vigorous and extensive root systems, can explore large soil volumes and absorb more water and nutrients under nutrient stress conditions and can increase crop yield and nutrient use efficiency (Merrill et al., 2002). The quantity of nutrient taken up by plants is largely influenced by root radius, mean root hair density and length of root (Barber, 1995). The shape and extent of root systems influences the rate and pattern of nutrient uptake from soil. Vose (1990) states that rooting depth; lateral spreading, branching and number of root hairs has major impact on plant nutrition. The configuration of root system is influenced markedly by nutrient supply. Mineral excess and deficiency affects growth (dry mass, root: shoot ratio) and morphology (length, thickness, surface area, density) of roots and root hairs. Nutrient deficiency leads to much finer roots. When plants are N deficient their roots branch more in regions where the soil is locally enriched with N (Scott-Russell, 1977). The configuration (root

and root hair abundance and density, distribution, effective radius and elongation) of root systems, in relation to nutrient uptake is extensively covered in an earlier paper by Barley (1970). The amount of carbon (C) and N supplied by roots can be significant for maintaining or improving soil organic matter and influencing nutrient use efficiency (Sainju et al., 2005). A well developed root system may play a dominant role in soil C and N cycles (Gale et al., 2000; Puget and Drinkwater, 2001) and may have relatively greater influence on soil organic C and N levels than the aboveground plant biomass (Boone, 1994; Norby and Cotrufo, 1998). Roots can contribute from 400 to 1460 kg C ha<sup>-1</sup> during a growing season (Qian and Doran, 1996; Kuo et al., 1997). Liang et al. (2002) found that maize roots contributed as much as 12% of soil organic C, 31% of water soluble C, and 52% of microbial biomass C within a growing season. All of these chemical and biological changes in soils affected by root systems improve nutrient use efficiency in plants.

Cultivar differences in root size are quite common and have been related to differences in nutrient uptake (Caradus, 1990; Baligar et al., 1998; Fageria et al. 2006a). Differences between white clover (*Trifolium repense* L.) populations and cultivars in P uptake per plant at low levels of P have been related to differences in root size and absolute growth rate (Caradus and Snaydon, 1986). Data in Table 4 show that root dry weight of common bean (*Phaseolus vulgaris* L.) genotypes varied from 1.54 to 3.14 g per 3 plants a variation of 2 fold at 0 mg K kg<sup>-1</sup> of soil. At the 200 mg K kg<sup>-1</sup> level, root dry weight varied from 1.50 to 2.30 g per 3 plants, a variation of 1.5 fold. Similarly, maximum root length varied from 42 to 46 cm at low K level and 32 to 44 cm at higher K level. At the higher K level, there was a slight decrease in root length of all the genotypes and root weight of 3 genotypes also decreased at the higher K

Table 4

Root dry weight and maximum root length of six common bean genotypes as influenced by potassium levels applied to a Brazilian Oxisol

Genotypes	0 mg K kg <sup>-1</sup>		200 mg K kg <sup>-1</sup>	
	Root dry weight (g/3 plants)	Maximum root length (cm)	Root dry weight (g/3 plants)	Maximum root length (cm)
Apore	1.54	45	1.67	32
Perola	1.97	42	2.04	39
Ruda	1.94	44	2.30	35
IAC Carioca	3.14	45	1.70	38
Jalo Precoco	2.24	42	1.67	36
Safira	1.77	46	1.50	44
Average	2.10	44	1.81	37

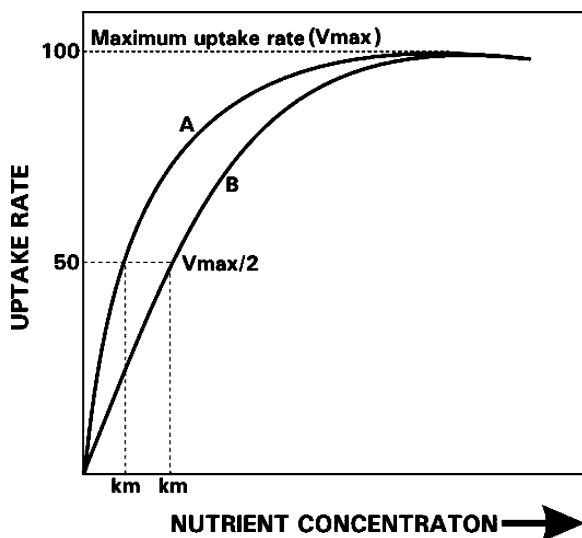
Values were determined at physiological maturity.

Source. Fageria, unpublished data.

level. However, at the higher K level, there were more root hairs than at the low K level (visual observations). There is widespread evidence for genotype diversity in root characteristics of many crops in response to environment and increasing interest in using this diversity to improve agricultural production and consequently, nutrient use efficiency (Gregory, 1994; Barber, 1994). Mineral deficiency and toxicity, mechanical impedance, moisture stress, oxygen stress and temperature have tremendous effects on root growth, development and function and, subsequently the ability of roots to absorb and translocate nutrients (Barber, 1995; Marschner, 1995; Baligar et al., 1998; Mengel et al., 2001). Mineral deficiency induces considerable variations in growth and morphology of roots, and such variations are strongly influenced by plant species and genotypes. Overall, the growth of the main axis is little affected by nutrient deficiency, but that of lateral branches and their elongation rates appear to be substantially reduced. Baligar et. al. (1998) summarized effects of various essential elements as follows: nitrogen deficiency increases root hair length, increases or has no effect on root hair density, and reduces branching; P deficiency increases overall growth of roots and root hair length, increases number of second-order laterals and either increases or does not affect root hair density, K and Ca deficiencies reduce root growth, however higher Mg levels reduce the dry mass of roots. These nutrient stress factors on nutrient efficiency in plant have not been well explored. Baligar et al. (1998) states that low pH reduces root mass, length and root hair formation, in alkaline soils ammonium toxicity causes severe root inhibition and in general salinity leads to reduction in mass and length of roots and dieback of laterals.

### Higher Rate of Nutrient Absorption at Low Rhizosphere Concentrations

Capacity of some plant species or genotypes within species to absorb nutrients at higher rate at low nutrient concentration of the growth medium is one of the mechanisms responsible for efficient nutrient use by plants. The  $V_{\max}$  and  $K_m$  values according to Michaelis-Menten kinetics or enzyme kinetics are generally used to explain the rate of ion influx in plant roots (Barber, 1995). According to this hypothesis, when nutrient uptake rate is plotted against nutrient concentration, a quadratic response or increase is obtained and maximum rate of uptake is designated as  $V_{\max}$  (Y-axis). Half of the maximum velocity line touching the uptake rate curve and corresponding concentration on the (X-axis) is designated by  $K_m$ . Lower  $K_m$  values (higher affinity), indicates a higher uptake rate of plants for a determined nutrient at low concentration. Figure 6 shows different uptake rates and  $K_m$  values of two genotypes designated A and B. Although the two genotypes have similar  $V_{\max}$  values, genotype A has a lower  $K_m$  value than genotype B, and hence genotype A will have higher uptake rates at low rhizosphere nutrient concentrations. In this case, genotype A is more efficient in nutrient uptake at lower rhizosphere nutrient concentration. Table 5 shows  $K_m$  values for P uptake by various plant species and P uptake rate was



**Figure 6.** Hypothetical relationship between nutrient concentration and uptake rate in two genotypes and their  $K_m$  and  $V_{max}$  values.

in the order of peanut (*Arachis hypogaea* L.) > rice > alfalfa (*Medicago sativa* L.) > corn > Barley > wheat.

### Ability of Plant to Solubilize Nutrients in Rhizopere

Several chemical changes occur in the rhizosphere, due to plant roots and soil environmental interactions. Among these changes, pH, oxidation potential,

Table 5

Michaelis-Menten constants for the absorption of phosphorus by principal crop species in nutrient solution

Crop species	Range of P concentration ( $\mu\text{M}$ )	$K_m$ in Mole (M) at low concentration	Reference
Barley	1–1000	$5.4 \times 10^{-6}$	Andrew (1966)
Peanut	0.03–400	$0.6 \times 10^{-6}$	Alagarswamy (1971)
Alfalfa	100–1000	$2.0 \times 10^{-6}$	Baligar (1987)
Alfalfa	1–500	$4.3 \times 10^{-6}$	Andrew (1966)
Wheat	0.1–1000	$7.4 \times 10^{-6}$	Edwards (1970)
Rice	0.1–161	$2.5 \times 10^{-6}$	Fageria (1973)
Rice	0.6–161	$1.4 \times 10^{-6}$	Fageria (1974)
Corn	100–1000	$2.2 \times 10^{-6}$	Baligar (1987)

rhizodeposition, nutrient concentrations and root exudates are prominent. These chemical changes in the rhizosphere significantly influence nutrient solubility and uptake by plants. Soil pH is one of the most important chemical properties, influencing nutrient solubility, and hence availability to plants. At lower pH (<5.5), availability of most micronutrients is higher except Mo and decreases with increasing soil pH. This decrease is mostly associated with adsorption and precipitation processes. Availability of N as well as P is lower at lower pH and is improved in a quadratic fashion with increasing pH to about 7.0. The increase in N availability is mainly associated with improved activity of N turnover by bacteria. The availability of P is associated with neutralization of aluminum (Al), manganese (Mn), and iron (Fe) compounds that immobilize this element at lower soil pH.

It is well known that acidification of the rhizosphere can solubilize several low soluble macronutrients (Riley and Barber, 1971; Barber, 1995) and micronutrients (Marschner, 1995; Hinsinger and Gilkes, 1996; Fageria et al., 2002). Bar-Yosef et al. (1980) reported that root excretion of hydrogen ( $H^+$ ) at the root surface is a mechanism for enhancing Zn uptake than excretion of complexing agents. When more cations are absorbed,  $H^+$  ions are released in the rhizosphere and pH decreases and when more anions are absorbed, hydroxide ( $OH^-$ ) ions are released and pH increases (Barber, 1995; Mengel et al., 2001). The release of  $H^+$  and  $OH^-$  ions in the rhizosphere associated with maintaining cation and anion balance in plants during the ion uptake process. Enhanced reducing activity at root surfaces has been noted as root-induced responses to Fe deficiency in dicotyledonous and nongraminaceous monocotyledonous plants (Marschner, 1995).

Root activity alters rhizosphere redox potential through respiratory oxygen consumption and ion uptake or exudation. In particular, root absorption and assimilation of ammonium ( $NH_4^+$ ) and nitrate ( $NO_3^-$ ) consume 0.31 mol oxygen ( $O_2$ ) per mol of  $NH_4^+$  and 1.5 mol  $O_2$  per mol of  $NO_3^-$ , respectively (Bloom et al., 1992). Hence, when roots use  $NO_3^-$  as a nitrogen source, the rhizosphere redox potential declines more rapidly than when they use  $NH_4^+$  (Bloom et al., 2003). The concentration of  $NH_4^+$  and  $NO_3^-$  in the rhizosphere and rhizosphere redox potential may be partially responsible for the observed large fluctuations in the relative availability of soil  $NH_4^+$  and  $NO_3^-$  and in root growth (Jackson and Bloom, 1990).

Many other nutrient solubility or uptake processes occurs in the rhizosphere, and alter redox potential. Redox reactions involves forms of Mn ( $Mn^{2+}$  and  $Mn^{4+}$ ), Fe ( $Fe^{2+}$  and  $Fe^{3+}$ ), and copper (Cu) ( $Cu^+$  and  $Cu^{2+}$ ) (Lindsay, 1979). However, the Fe and Mn redox reactions are considerably more important than those of Cu because of their higher concentrations in soil (Fageria et al., 2002). The primary source of electrons for biological redox reactions in soil is organic matter, but aeration, pH, and root and microbial activities also influence these reactions. Redox reactions in rhizosphere can also be influenced by organic metabolites produced by roots and microorganisms.

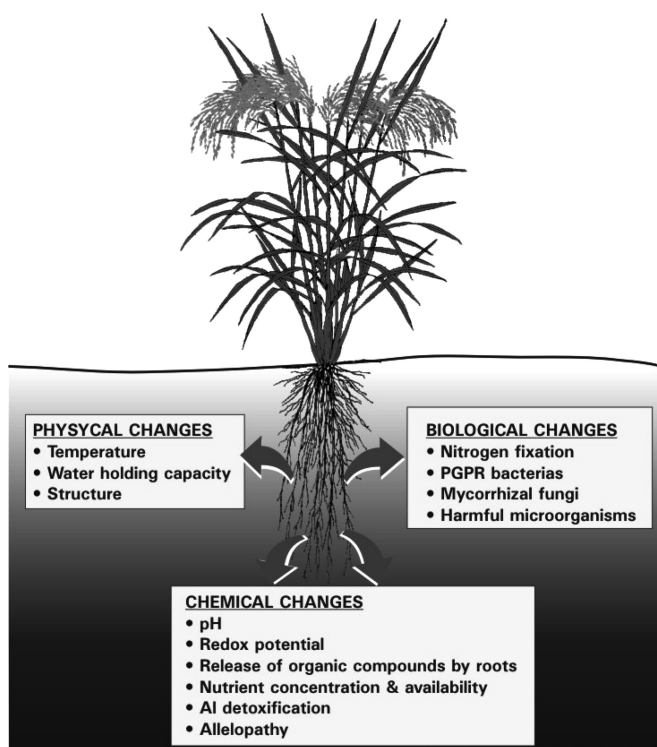
Iron efficient plants have the ability to respond to iron deficiency stress by activating biochemical reactions that release compounds (phytosiderophores) to enhance Fe uptake (Bienfait, 1988; Marschner, 1995). Reduction of rhizosphere pH due to root  $H^+$  excretion, root exudation of organic acids (mainly phenolics), enhanced root reduction of  $Fe^{3+}$  to  $Fe^{2+}$ , and activated root-reducing capacity at cell plasma membranes are responsible for overcoming Fe deficiency by dicotyledonous plants. In general,  $C_3$  species are more productive under Fe-deficiency stress than  $C_4$  species (Duncan and Carrow, 1999).

Root induced rhizosphere chemical changes have been reported to increase availability of P to pigeon pea (*Cajanus cajan* L. Mill sp.) (Ae et al., 1990). Roots of this plant release piscidic acid, which complexes Fe and thereby free some of the tightly bound soil P. Hence, pigeon pea is successfully grown in P deficient tropical soils (Radin and Lynch, 1994). Keerthisinghe et al. (2001) reported that white lupin (*Lupinus albus* L.) and pigeon pea have the ability to access fixed P and this is attributed to the exudation of organic acids into the rhizosphere. Under P-limiting conditions, white lupin exudes large quantities of citrate and pigeon pea responds by increased exudation of malonic and piscidic acids. These organic acids increase the availability of P in acid soils, mainly by chelation of Al and Fe bound to P and by suppressing readsorption and precipitation of organic P. Major physical, chemical and biological changes occurring in the rhizosphere are summarized in Figure 7. Extensive discussions of chemical changes in the rhizosphere and nutrient availability are given by Baligar et al. (1990), Darrah (1993), Barber, (1995), Marschner, (1995), Hinsinger (1998), Fageria and Stone (2006), and Fageria et al. (2002).

### Better Distribution and Utilization of Nutrients within Plant

Better distribution of nutrients in parts of plant (root, shoot and grain) reflects their use efficiency. In recent years, there have been major increases in the average yields of most crops. Most of these increase in yields have been accompanied by increase in plant tissue having high nutrient content such as grain compared to the lower nutrient content straw (Atkinson, 1990). Higher accumulation of N and P in grain improves yield and consequently leads to higher use efficiency of these nutrients (Fageria et al., 2006a). The proportion of total plant N or P partitioned to grain is called N or P harvest index. Nutrient harvest index is defined as nutrient uptake in grain divided by nutrient uptake in grain plus straw. This index is very useful in measuring nutrient partitioning in crop plants, which provides an indication of how efficiently the plant utilized acquired nutrients for grain production (Fageria and Baligar, 2005). High nitrogen or P harvest index is associated with efficient utilization of N (Fawcett and Frey, 1983; Rattunde and Frey, 1986; Fageria et al., 2006a).

Schmidt (1984) pointed out that new cultivar development may need to be directed towards the production of genotypes that exploit inputs most efficiently,

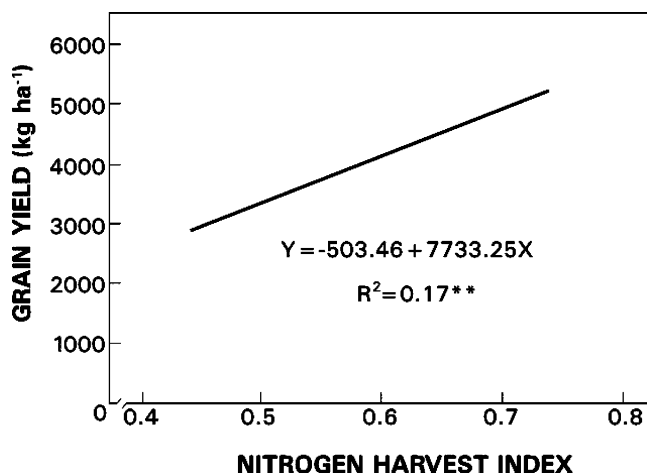


**Figure 7.** Physical, chemical and biological changes in the rhizosphere. *Source:* Fageria and Stone (2006).

not on genotypes that have superior yield only when high production inputs are used. Isfan (1993) reported that physiological efficiency of absorbed N (ratio of grain produced to the total N absorbed by the above ground plant parts) may be used in a plant breeding program to detect potentially high yielding oat genotypes and to evaluate those capable of exploiting N input most efficiently. The physiological efficiency index of N is related to many physiological processes such as absorption nitrate reduction efficiency, nitrogen remobilization, translocation, assimilation and storage (Novoa and Loomis, 1981). Figure 8 shows a relationship between N harvest index ( $NHI = N \text{ uptake in the grain} / N \text{ uptake in the grain plus straw}$ ) and grain yield of lowland rice. Grain yield increased linearly with increasing nitrogen harvest index within the range of 0.44 to 0.74.

Amounts of N or P remobilization from storage tissues influence grain N or P use efficiency and this varies among genotypes and appears to be under genetic control (Moll et al., 1982; Dhugga and Waines, 1989). Variation in nutrient harvest indices among crop species, or genotypes of the same species, is a useful trait in selecting crop genotypes for higher grain yield (Fageria and Baligar, 2005). Dhugga and Waines (1989) reported that genotypes that





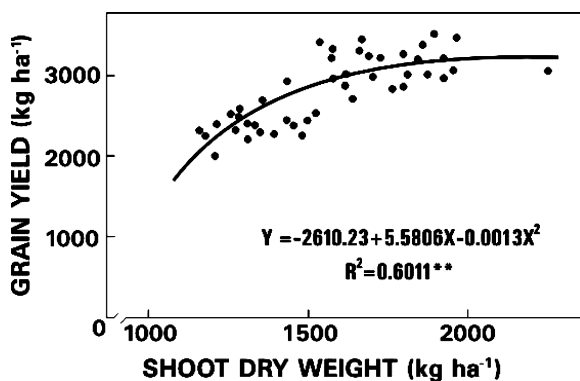
**Figure 8.** Relationship between nitrogen harvest index and grain yield of lowland rice. Values are averages of five genotypes. *Source:* Fageria, unpublished data.

accumulate little or no N after anthesis had low grain yields and low nitrogen harvest index.

Moll et al. (1982) reported that eight single cross corn hybrids differed in N-efficiency traits and yield when grown in the field with low and high soil N. At low soil N, hybrid differences in N-use efficiency were due to largely to variation in utilization of acquired N. At high soil N, hybrid differences were attributed to variation in N uptake efficiency. Differences in N translocation and remobilization to the grain were important only at low levels of soil N (Clark and Duncan, 1991). Inter-intra specific differences for nutrient use efficiency for macro and micro nutrients for sorghum (*Sorghum bicolor* L.), maize, alfalfa (*Medicago sativa* L.), and red clover (*Trifolium pretense* L.) have been reported (Baligar and Fageria, 1997).

### Better Allocation of Dry Matter within Plants

Better distribution of dry matter in crop plants (shoot and grain) is generally associated with higher yields and consequently, higher nutrient uses efficiency. While the production and utilization of dry matter within a plant depend on each other, the regulation of the partitioning of dry matter into different plant parts is independent of the production of assimilate (Ho, 1988). This means, partitioning of assimilate is genetically determined in crop plants. However, it is also influenced by environmental factors. Dry matter distribution is measured by grain harvest index (GHI). The GHI is the ratio of grain yield to total biological yield and calculated with the help of the equation:  $GHI = (\text{grain yield} / \text{grain} + \text{straw yield})$ . The term GHI was introduced by Donald (1962), and since has



**Figure 9.** Relationship between shoot dry weights and grains yield of common bean grown on an Oxisol. *Source:* Fageria, unpublished data.

been considered an important trait for yield improvement in field crops. Values for GHI in cereals and legumes are normally less than 1. Although GHI is a ratio, it is sometimes expressed as a percentage.

Generally, dry matter is positively associated with grain yield (Fageria et al., 2004a). Figure 9 shows that grain yield of common bean increased significantly and quadratically with increasing shoot dry weight. Evans (1993; 1994) reported that yield increases in many cereals, legumes and root crops during the 20th century were due to increase in harvest indexes of these crops. Austin (1994) reported that in rice, wheat and barley, modern cultivars are short in stature and can have a grain harvest index near 0.50. In contrast, old cultivars are taller and have harvest indices of 0.30 or lower. Hay (1995) reported that grain harvest index of grain crops, particularly cereals, has increased with increasing crop yields during the last 50 years of the 20th century. However, plant breeders have not sought to raise grain harvest index, and probably any increase in this trait has been an unplanned secondary effort of breeding for grain yield (Araujo and Teixeira, 2003).

The GHI values of modern crop cultivars are commonly higher than those of old traditional cultivars for major field crops (Ludlow and Muchow, 1990). Genetic improvement in annual crops such as wheat, barley, corn, oat, rice and soybean (*Glycine max* L. Merr.) has been reported due to increase in dry weight as well as GHI (Austin et al., 1980; Wych and Rasmusson, 1983; Wych and Stuthman, 1983; Cregan and Yaklich, 1986; Payne et al., 1986; Tollenaar, 1989; Feil, 1992; Peng et al., 2000). In potato (*Solanum tuberosum* L.), modern cultivars have plant dry weights 10 times that of the wild species (*Solanum demissum* L.). Harvest index (tuber dry weight as a proportion of plant weight) increased from 7% in wild species to 81% in modern cultivars (Inoue and Tanaka, 1978). Peng et al. (2000) reported that genetic gain yield of rice cultivars released before 1980 were mainly due to improvement in GHI, while increases

in total biomass were associated with yield trends for cultivars developed after 1980. Cultivars developed after 1980 had relatively high GHI values, but, further improvement in GHI was not achieved. These authors also reported that further increases in rice yield potential would likely occur through increasing biomass production rather than increasing GHI.

### Balanced Source and Sink Relationship

Genetic and production physiological studies show that crop yield potentials are high and they are not fully exploited (Fageria et al., 2006a). Balanced source and sink relationships were vital for higher yields and, consequently, higher nutrient use efficiency in crop plants. However, neither source nor sink manipulation alone can improve crop yield indefinitely (Ho, 1988). Most plants have the ability to buffer any imbalance between source and sink activity by storing carbohydrate during periods of excess production and mobilization of these reserves when the demands of growth exceed the supply of carbohydrate available through current photosynthesis (Evans and Wardlaw, 1996). Both source activity and sink activity vary with plant development and are modified by environmental factors.

Biomass production in plants depends on photosynthesis. In the beginning of plant growth, leaves function as sinks but with advancement of age serves as sources. Hence, leaves are main site of photosynthesis and source of carbohydrate in plants; however, with advances in plant age, stems and inflorescence of some of cereals contribute substantially to photosynthetic activity (Evans and Wardlaw, 1976). Evans and Wardlaw (1996) reported that photosynthesis by glumes and young grains of wheat constitute an important source of assimilate as well as a means of recapturing respired carbon dioxide ( $\text{CO}_2$ ). Ear photosynthesis throughout grain growth contributed 33% to grain growth requirements in one awned wheat cultivar and 20% in an unawned one (Evans and Rawson, 1970).

Panicles or heads in cereal, pods in legumes and tubers in root crops are main sinks of photoassimilates. A small portion of photosynthetic product is also translocated to roots. Growing organs of plant are active sinks and these prevent accumulation of photoassimilates in the sources, if source capacity is limited. Assimilated carbohydrates in the source as well as sink are lost through respiration and this loss is reportedly half of the total carbon assimilated in photosynthesis. (Evans and Wardlaw, 1996). In modern cultivars, source capacity has been more limiting to yield than in the older ones (Evans and Wardlaw, 1996). During the 20th century, both source and sink have been improved in important annual crops and this made possible an improvement in yields (Ho, 1988). The capacity of dry matter production in leaves may either be higher or lower than the capacity of dry matter accumulation in other parts of the plant. Hence, at different times, either source or sink limiting situations may exist in crop production (Ho, 1988).

## ROLE OF CROPS IN IMPROVING NUTRIENT USE EFFICIENCY UNDER BIOTIC AND ABIOTIC STRESSES

Abiotic (soil acidity, soil salinity/alkalinity, drought, water logging, high temperature, and mineral deficiency/toxicities), and biotic (diseases, pests, and weeds) stresses have tremendous effects on plant growth and development and ability to take up and utilize nutrients more efficiently (Pessarakli, 1999; Alam, 1999; Baligar et al., 2001). Nutrient use efficiency and yield of crops under stress could be enhanced by selection/breeding of plants that have high nutrient use efficiency (acquisition, influx, transport, utilization, and remobilization), and ability to interact effectively with environmental extremes (drought, solar radiation, and temperature extremes). Plant species and genotypes/ cultivars within species differ in optimal environmental requirements and their abilities to tolerate a particular stress.

In addition to low soil fertility, soil acidity is a serious problem worldwide. Soil acidity decreases crop productivity and nutrient use efficiency in crop plants. Reasons for poor crop productivity in acid soils are: presence of elemental toxicities (Al, Mn, Fe, H) and deficiencies or unavailability of essential nutrients [N, P, calcium (Ca), magnesium (Mg), K, Fe, Zn], physical constraints (compaction, hard pan), degraded and infertile soils (erosion, leaching and gaseous nutrient losses, low microbial activities), low recovery efficiency of applied nutrients during a single season (<50% for N, <20% for P, 40-70% for K, micronutrients 5-10%) (Mortvedt, 1994; Raun and Johnson, 1999; Fageria, 2000; Fageria and Baligar, 2001; Fageria and Baligar, 2005), inadequate/non use of soil amendments (lime, fertilizers), adverse environmental conditions (high temperature, low rainfall, and high ET), existence of low plant species or cultivar tolerance to soil acidity, low potential for plant growth and nutrient use efficiency (NUE), planting of nonacid tolerant plants with inefficient NUE, and high intensity of weeds, insect and diseases (Baligar and Fageria, 1997, 1999).

Liming acid soils is a dominant and effective practice for improving crop yields, and consequently, nutrient use efficiency. Lime reduces toxic effects of hydrogen, aluminum and manganese, improves soil biological activities, cation exchange capacity (CEC), P, Ca and Mg availability and soil structure, promotes N<sub>2</sub> fixation, stimulates nitrification, and decreases availability of K, Mn, Zn, Fe, boron (B), and Cu. Figure 3 shows that in a Brazilian Oxisols common bean yield increased significantly and quadratically with increasing soil pH. Low pH (excess Al), reduces root elongation and lateral root growth and greatly affects the absorption of nutrients. However, use of acid tolerant crop species and genotypes within species, in combination with lime is an important strategy for reducing cost of crop production on acid soils. Variation in acidity or Al tolerance among different crop species and genotypes of same species has been widely reported (Foy, 1984; 1992; Baligar and Fageria, 1997, 1999; Kochian, 1995; Fageria et al., 2004b; Yang et al., 2004). Grain yield of upland rice and soil chemical properties is significantly and negatively correlated with pH, Ca saturation

Table 6  
Correlation coefficients (r) between grain yield of 20 upland rice genotypes and soil chemical properties across two acidity levels

Soil chemical property	r values
pH in H <sub>2</sub> O	−0.23*
Ca saturation (%)	−0.21*
Base saturation(%)	−0.21*
Al (mmol <sub>c</sub> dm <sup>−3</sup> )	0.19*
H+Al (mmol <sub>c</sub> dm <sup>−3</sup> )	0.23*

\*Significant at the 5% probability level.

Source: Adapted from Fageria et al. (2004b).

and bases saturation and is significantly and positively correlated with Al, and H+Al (Table 6). Upland rice genotypes evaluated in this study were tolerant to soil acidity. Hence, developing soil acidity tolerant crop species or cultivars of the same species also deserves logical consideration during the 21st century.

Plant species and genotypes/cultivars within species differ widely in tolerance to soil acidity constraints (Foy, 1984, 1992; Baligar and Fageria, 1997, 1999). Acid soil tolerance of crop plants generally involves more than one mechanism. For example, plasma membrane/cell wall exclusionary responses via selective permeability/polymerization, pH barrier (chelating ligands or mucilage) formation at root-soil interface, internal chelation by organic acids (carboxylic, citric, malic and transaconitric) or metal binding proteins and enzymes and vacuole compartmentation of Al or Mn are involved (Duncan, 1994; Duncan and Carrow, 1999; Yang et al., 2004). Soil acidity constraints also reduce uptake of certain essential elements and increase of others. (Foy, 1984; Baligar and Fageria, 1997, 1999). Soil acidity tolerant plant species and genotypes, are efficient in absorption and utilization of nutrients (Baligar and Fageria, 1997, 1999). Foy (1984) lists the following mechanisms that plants have developed to maintain their nutrient requirements and to overcome soil acidity constraints: raise the rhizosphere pH to reduce the toxic levels of Al, Mn, and H, increase microbial activities to enhance organic matter decomposition, thereby release inorganic nutrients for plant use, and improve root rhizobial associations thereby increasing nitrogen fixation, and efficient nutrient use efficiency for N, P, Ca, Mg, and K.

Saline soils contain an excess of neutral salts such as chloride and sulfates of Na<sup>+</sup>, K<sup>+</sup>, Ca<sup>2+</sup>, and Mg<sup>2+</sup> (Mengel, et al., 2001). In saline soils plants are affected by water deficit, ion toxicity [chloride (Cl), sodium (Na)] and nutrient imbalances due to depression in uptake and transport. (Grattan and Grieve, 1999a; 1999b). In alkaline soils Fe deficiency, B toxicity and salinity are the most obvious problems for successful crop production. Salinity reduces root growth and permeability and consequently reduces water and nutrient

uptake. Large differences in salt tolerance have been reported for plant species and cultivars within species (Maas, 1986; Marschner, 1995). Saline conditions greatly affect availability in soil, movement to root surface, uptake and transport and partitioning of N, P, K, Ca, Mg, and micronutrients (Grattan and Grieve, 1999a, 1999b). By selection and breeding of soil alkalinity and salinity tolerant plant species and cultivars within species, along with improved best management practices to reduce salinity and alkalinity in soil, it is possible to achieve reasonable crop yields in high pH soils. Differences in tolerance to salinity have been reported among genotypes of maize, bean and other species (Foy, 1992). Plant development and successful crop production in salt affected soils depends on improved supply of adequate water and nutrients. Adapting soil management practices to reduce salt levels, improving water and nutrient status and selection or breeding of salt tolerant species and cultivars are effective in improving nutrient use efficiency and crop yields in salt affected soils. Epstein and Bloom (2005) have covered physiology of salt stress, further they state that mechanisms of salt tolerance and its genetic and molecular feature are currently under intense development and knowledge developed could be useful in the future in breeding of salt-tolerant crops.

Poor crop productivity in many soils of the world is due to deficiencies of essential elements and toxicities of metal elements. Inter- and intraspecific variations for plant growth and mineral composition have been well documented (Clark, 1990; Epstein and Jefferies, 1964; Vose, 1984; Gerloff and Gabelman, 1983). Genetic and physiological components of plants have profound effects on their abilities to absorb and utilize nutrients under various environmental and ecological conditions. Clark (1990) has covered extensively the mechanisms involved for genotypic variation in mineral nutrient uptake and utilization. Mineral deficiency and toxicity stress have major affect on root growth and morphology (number, diameter, length, surface area and distribution in soil) (Baligar et al., 1998). Such changes in root morphology and growth will have effects on plant ability to take-up nutrients effectively from soil. Clark and Duncan (1993) suggested use of juvenile stage of plant growth in selection for mineral stresses and most common trait is yield (vegetative or grain). Best management strategy for over coming mineral stressed soil is to select/ improving plants for production on abiotic stressed soils with limited soil amendments (Clark and Duncan, 1993).

During the growth cycle, plants are subjected to drought (water deficit) of a very short period or longer in duration. Water stress during growth cycles of plants adversely affects many physiological growth process (photosynthesis, translocation of carbohydrates and growth regulators, ion uptake transport and assimilation, N<sub>2</sub> fixation, turgidity, respiration) and shoot and root morphology and growth (cell enlargement, leaf area, root growth and extension) (Fageria et al., 2006a). Water stress is primarily responsible for stomatal closure there by reducing assimilation and growth. Water stress reduces plant growth by reducing cell division and root enlargement and leads to a decline in ion transport to

the root surface. In dry soil nutrients are less mobile mainly because pores are filled with air and pathways for nutrient flux from soil to root surface are less direct. Such conditions in soil limit ion flux to root surface by diffusion and mass flow (Barber, 1995; Pugnaire et al., 1999). Extent of drought injury to plants depends on the length of drought and nature of species and cultivars/genotypes within species involved. Plants are known to have drought escape, drought avoidance or tolerance components to overcome drought injury. Species and varieties differences in drought avoidance are attributed to: lower transpiration rate, rapid stomatal closure, ability to retain a high percentage of water, greater water uptake, greater root volume, higher root-shoot ratio. Drought tolerance is attributed to avoidance of dehydration of guard cells, hydration tolerance of photosynthesizing cells, and decreased rate of protein loss. In plant selection process for drought tolerance, the morphological drought escape and avoidance and tolerance features in plants need to be harnessed (Baligar and Duncan, 1990). Among various factors temperature is the major uncontrollable factor, which has great impact on crop growth and production. Plant has adapted tolerance or avoidance mechanisms to overcome heat stress. High temperature stress leads to an insufficient supply of carbohydrates to root meristems, where as low temperature leads to poor or reduced shoot growth due to an insufficient supply of mineral nutrients and water (Marschner, 1995). Temperature extremes, nutrient availability and uptake are inhibited in addition to reduction in root growth. Epstein and Bloom (2005) state that with rises in temperature alters integrity of biological membrane. At high temperature nutrient influx cannot keep pace with nutrient efflux that leads to increased nutrient leakage from roots. Low temperature reduces growth of shoots and roots and mineral nutrition of plants (Bowen, 1991; Cooper, 1973). Inter-and intraspecific differences in plant dry matter yields mineral composition and nutrient use efficiency at varying temperature have been reported (Cooper, 1973, Bowen, 1991; Baligar et al., 1997).

Nutrient levels and their availability to plants in soil may affect plant susceptibility to insects and diseases. Plant diseases are greatly influenced by environmental factors, including deficiencies and /toxicities of essential nutrients, and balanced nutrition has an important role in determining plant resistance or susceptibility to diseases (Fageria et al., 1997). Global preharvest crop losses due to pathogens are 9 to 15% of annual production. Mineral elements are directly involved in plant defense mechanisms as integral components of cells, substrates, enzymes, and electron carriers or as activators, inhibitors and regulators of metabolism (Huber, 1980). Nutrient stressed plants are often more susceptible to disease than those at a nutritional optimum, yet plants receiving a large excess of a required mineral may become predisposed to disease. Fageria et al. (1997) summarized the nutrient element role in disease intensity in plants as: (i) high N increases plant susceptibility to obligate pathogens, but decreases their susceptibility to facultative pathogens; (ii) application of K, Ca, Mn, Fe, B, Cu, and silicon (Si) to soil deficient in these elements usually increases

the resistance; however, the effects of P and Zn are variable and there is not sufficient information available on Mg and S to reach definite conclusions; and (iii) deficiency ranges of micro nutrients are known to decrease disease resistance. Copper, B, and Mn are involved in synthesis of lignin, and simple phenols and Si create physical barriers to pathogen invasion. The greatest benefits from nutrients are found with moderately susceptible or partially resistant cultivars. Salinity induces metabolic changes such as accumulation of proline, glycine-betaine,  $\text{Na}^+$  and  $\text{Cl}^-$  in plants such changes are known to reduce aphid feeding on plants (Araya, et al., 1991). Fageria and Scriber (2002) state that minerals and primary metabolites that are involved in basic plant processes are rarely considered responsible for plant resistance to insect attack, despite the major role they play in insect behavior. Overall, plants have lower average concentrations of N, sulfur (S), P, Fe, Zn, and Cu and have equal or greater concentrations of Mg, K, Ca, and Mn than insects (Schoonhoven et al., 1998). Seasonal variation, inter-intraspecific plant variations and environmental factors (soil type, fertilizer regime), influence concentrations of elements in plants. Some information is available concerning plant N content and how it alters mechanisms of plants resistance to insect herbivores; however information is lacking about the effects of other elements on insect herbivores (Fageria and Scriber, 2002). Overall, from the available data, it appears that the influence of levels of macro and micronutrients in plants may have positive negative or no effects on insect damage in crop plants (Fageria and Scriber, 2002). Biotic and abiotic factors are known to alter growth and elemental concentrations and modify plant resistance, but how such relations affect insect and diseases resistance in plant is not clearly understood. How insect attacks affect plants that have high NUE in the presence or absence of abiotic stress needs to be evaluated. Therefore, to overcome disease and insect pressure it is important to identify species and cultivars within species that are efficient in absorption and utilization of nutrients under abiotic stress. Such plant types will have greater ability to overcome abiotic stresses and achieve yield potentials.

There is need for establishing breeding programs to focus on developing cultivars with high NUE under specific stresses. Best management practices (BMP) such as use of fertilizer and amendment (lime), proper crop rotations, increases in organic matter content and control of erosion, insects, diseases and weeds can significantly improve crop yields and optimize nutrient use efficiency. The development of new cultivars with high NUE coupled with BMP's with an integrated pest management (IPM) strategy will contribute to economically viable and environmentally sustainable systems for the vast stress ecosystems of the world. Foy (1984, 1992) states that more emphasis should be given to plant-soil interactions and the breeding or selection of plants to fit the soils, and less emphasis should be placed on fitting all soils to meet demands of all plants. Fitting all soils to meet needs of all plant requires heavy input of amendments and fertilizers, which could increase cost of cultivation and accelerate environmental degradation.



## BREEDING FOR NUTRIENT USE EFFICIENCY

Selection and breeding nutrient efficient species or genotypes within a species is justified in terms of reduction in fertilizer input cost of crop production and also reduced risk of contamination of soil and water. Through plant breeding, the genetic yield potential of wheat, soybean, corn, and peanuts has been improved by 40-100% within the 20th century (Gifford et al., 1984; Ho, 1988). Genetic variability among crop species and genotypes of the same species for macro and micronutrients use or requirement is well documented (Clark and Duncan, 1991; Baligar and Fageria 1999, Baligar et al., 2001; Fageria and Baligar, 2005; Hillel and Rosenzweig, 2005). Micronutrients are required in small amounts by crops and their requirements can often be easily met by planting efficient genotypes. Micronutrient efficiencies of existing plant should be weighted against cost of breeding more efficient genotypes.

Considerable progress has been made in identifying crop species and genotypes within species for nutrient use efficiency, tolerance elemental toxicity and understanding possible mechanisms involved (Graham, 1984; Maas, 1986; Clark and Duncan 1991, Foy, 1984, 1992; Baligar et al., 2001; Blamey, 2001; Marschner, 1995, Okada and Fischer, 2001; Fageria et al., 2003; Yang et al., 2004; Epstein and Bloom, 2005; Fageria and Baligar, 2005; Fageria et al., 2006a). Plant traits and characteristics showing tolerance to essential nutrient deficiencies is numerous, have been reviewed (Baligar et al. 1990). Clark and Duncan (1993) suggested that juvenile stage of plant growth is more desirable to evaluate plants for mineral stress tolerance. Further they state that yield (vegetative or grain/seed/fruit) probably the most common traits used to evaluate plants for tolerance to soil mineral stresses. However, progress has been limited in releasing crop cultivars having these traits. One good example of solving nutrient deficiency problem with breeding involves iron deficiency. This problem in calcareous soils has been overcome by selecting/breeding iron efficient genotypes of corn, soybean, sorghum and rice (Graham, 1984). When Brazilian Oxisols were limed a pH above 6.0, for growing legume crops such as common bean and soybean, iron precipitated and created Fe deficiency in a subsequent upland rice crop (Fageria et al., 2003). These soils are well supplied with iron, however, at higher pH (>6.0) iron is precipitated and its availability is low (Fageria et al., 2003). Under these conditions Fe availability is improved by decreased pH, reducing conditions and Fe chelators, root exudates by Fe efficient genotypes (Graham, 1984).

Induced iron deficiency chlorosis is widespread and is a major concern for plants growing on calcareous or alkaline soils due to their high pH and low availability of iron (Welch et al., 1991; Marschner, 1995). Planting iron efficient genotypes is the best solution for correcting iron deficiency under these situations (Fageria et al., 2003). Iron efficiency can range from monogenic to polygenic control, depending on species (Duncan, 1994). Both additive and dominant gene actions may be involved (Duncan and Carrow, 1999).

Breeding of more efficient plants for major nutrients such as N, P, and K, which are required in large amounts by crop plants for maximum economic yield, requires special attention. Authors and coworkers have conducted several field and greenhouse experiments using genotypes of rice, wheat and common bean in Brazilian Inceptisols and Oxisols using different N and P rates (Fageria, 1998; Fageria, 2000; Fageria and Baligar, 1997b; 1999; Fageria and Barbosa Filho, 2001; Fageria et al., 2001). In these studies inter and intra specific differences were observed for growth and N and P use efficiency. When P level in the soil extracted by Mehlich 1 extracting was around 2 mg kg<sup>-1</sup> of soil, either most of the genotypes did not produce or produced insignificant grain yield. Similarly, without addition of N fertilizers, rice genotypes produced very low grain yield. Hence, the strategy should be to use efficient crop genotypes along with judicious use of N, P and K fertilizers.

In addition, although numerous studies have shown wide range of genotypic differences among and within species for N, P, and K efficiency traits, the genetics of these plant responses are not well understood and appear to be complex (Clark and Duncan, 1991). Most studies indicated a genetic control. Heritabilities of some N efficiency traits were relatively high while others were low (Clark and Duncan, 1991). Clark and Duncan (1991) reported that P efficiency traits are heritable, and could be used to improve germplasm for P nutrition. A prime example of success has been with white clover in New Zealand (Caradus, 1990). Root growth, morphology, ion uptake and use efficiency should be considered when plants are to be improved for mineral nutrition traits involving K in breeding programs (Pettersson and Jensen, 1983; Clark and Duncan, 1991). Yield has long been classified as a character controlled by quantitative genetics, i.e., one influenced by many genes with the effects of individual genes normally unidentified (Wallace et al., 1972). This means yield improvement by use of nutrient efficient genotypes deserves special attention in relation to identifying physiological components causing varietal differences in economic yield, and to acquire understanding of their genetic control. The high yields achieved in rice by incorporating short, erect, thick, dark-green leaves, and short stiff stems clearly demonstrate the merit of including physiological component traits in plant breeding programs (Wallace et al., 1972; Fageria et al., 2006a).

Richardson (2001) reported that soil P uptake can be increased by plant modification. Selection of plants for increased efficiency of P has been demonstrated with root morphology being particularly important (Lynch, 1995). Similarly, gene technologies offer opportunities for manipulating the structure and function of plant roots for improved acquisition of soil P (Richardson, 2001). Plant genes that regulate root branching have been isolated (Zhang and Forde, 1998) and the expression in plants of specific bacterial genes (i.e. encoding phytohormone activities) may offer new insights into the role of such genes in plant growth and development (Spena et al., 1992; Richardson, 2001). The cloning and characterization of plant and fungal phosphate transporter genes

may also provide new possibilities for increasing plant P uptake (Smith et al., 2000; Richardson, 2001).

Plant selection for sustained production in water-deficit environments has received considerable attention for three or four decades (Blum, 1993), yet genotypes/cultivar with substantial drought tolerance still remains elusive. Blum (1993) puts the plant varieties in to three categories: (a) those with uniform superiority over all environments; (b) those relatively better in poor environments; and (c) those relatively better in favored environment. However, so far no reliable genotypes or cultivar have evolved with considerable tolerance to drought. Progress in molecular biology to improve drought resistance/tolerance is restrained by ignorance in agronomy and crop physiology (Blum, 1993).

Molecular biology technology can be an important approach in isolation, identification, localization, and laboratory reproduction of gene(s) carrying desirable nutrient efficiency traits (Clark and Duncan, 1991). In the 20th century genetic engineering techniques did not play a significant role in improving nutrient efficient crop genotypes. However, its wide applicability or potential in the 21st century for improving nutrient efficiency in crop plants is highly predicted. In addition, recently, new possibilities have arisen to transfer desired traits (genes) not just between strains of the same species, but even from one species to another, thus greatly enlarging the range of potential genetic resources available to agricultural scientists (Hillel and Rosenzweig, 2005).

## CONCLUSIONS

Major factors, contributing to increased yields of annual crops during the 20th century, were improved cultivars, irrigation, nitrogen fertilizers, and control of diseases, insects or weeds. Spectacular gains in economic yield of rice, wheat, corn, barley and soybean have been achieved during 20th century and there is still much potential for increasing yield of these crops in the 21st century. Yields of modern cultivars is primarily source limited (supply of carbohydrates) and the source capacity should be increased, either genetically or by adopting appropriate cultural practices. More information should be generated about physiological and biochemical mechanisms involved in the efficient use of nutrients by crop plants. The use of biotechnology in identifying and creating nutrient efficient crop species or genotypes offers exciting potential. However, this needs to be put in appropriate perspective.

Abiotic stresses of acidity, salinity/alkalinity, mineral deficiencies, high temperature and water deficit continue to be major constraints for plant productivity throughout the world. Past practices of plant productivity under abiotic stresses have been to amend soil (fertilizer, lime, and gypsum) and to supplement water through irrigation to meet plant needs. However alternate strategy is to select/improve (breed) plants to overcome the abiotic stressed soils with limited amendment and water input.

Nutrient inputs in crop production systems have received special attention in recent years because of increasing fertilizer costs and concern about environmental pollution. Nutrients supplied by inorganic fertilizers make up the majority of plant nutrition requirements to sustain higher crop yields. Use of nutrient efficient crop species or genotypes within species in combination with other improved crop production practices offer the best option for meeting the future food requirements of expanding world populations. Research efforts are also needed to generate more information on correct assessment of nutrient deficiency/toxicity diagnosis in crop plants. Limited data are available on adequate rates, form and methods of nutrient application, and plant utilization efficiency, especially under field conditions.

Conventional and population breeding approaches have been successful in the 20th century and should continue to be important avenues of crop improvement programs in the 21st century. However, molecular genetic approaches, along with conventional plant breeding methods should be applied more vigorously in developing nutrient efficient crop species or genotypes/cultivars within species. Improved mineral nutrition traits in plants will help in reducing crop production costs and environmental pollution and should also benefit animal and human nutrition.

Nutrient use efficiencies have improved over time. This improvement was associated with increasing yield per unit area with better crop management practices and developing crop genotypes of higher yield potentials. In conclusion, use of inorganic fertilizers efficiently is essential in today's agriculture and will be even more important in years to come. Hence, nutrient efficient plants will play a vital role in increasing crop yields per unit area and improve health and quality of life of humans in the 21st century.

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